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SYSTEMATICS AND LIFE HISTORY OF SATURNIA (CALOSATURNIA) ALBOFASCIATA IN CALIFORNIA (SATURNIIDAE)

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Saturnia (Calosaturnia) albofasciata (Johnson, 1938) is unquestionably the least known saturniine of the United States. The species has received virtually no mention in the literature since its relatively late discovery and until 1950 was represented in collections by only three specimens. It is safe to say that even most North American lepidopterists are totally unaware that this moth exists.

Our interest (Hogue and Sala) in the species was originally aroused by a specimen in the Los Angeles County Museum (#9 below). Correspondence with J. W. Johnson during our earlier investigations of *Saturnia walterorum* (Sala & Hogue, 1958) made us aware that there existed a late fall saturniine in our local area that we knew nothing about. On the basis of the scant information then available we speculated on the life cycle of *S. albofasciata*. Our speculative conclusions proved to be valid in general. The life cycle is what makes this moth so interesting to us. No other saturniine in North America has such a cycle—spending the winter as an egg, spinning a cocoon and passing the summer months as a pupa and emerging and completing the imaginal stage just prior to the oncoming winter. The hemileucines have a cycle like this almost without exception but, of course, are not closely related to the saturniines.

RECORDS⁵

Type Material

The species was originally described (Johnson, 1938. Bul. Brook. Ent. Soc. 33:128-130) from two adult females as follows:

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⁵ All specimens recorded here are from California

- (1) Holotype ♀ : Clearlake Highlands, Lake County; on a porch screen. 31 October 1934; at noon (W. M. Hooton) [Calif. Acad. Sci., No. 4675].
- (2) Paratype ♀ : Sequoia National Forest, Tulare County. 1928 [E. Walter, Anaheim, California].

In a subsequent paper (1940, loc. cit. 35:46-50) Johnson described the male from a single specimen:

- (3) Plesio-allotype ♂ : ex. larva collected Lake County (exact locality unknown but probably near Clear Lake where the collector lived); on *Ceanothus cuneatus*. 23 or 28 May 1938, adult emerged 21 October 1938 (C. Macheboeuf) [Calif. Acad. Sci., No. 4908].

The account of the finding of the larva of this male has been related to us by J. W. Johnson (personal communication to Hogue — letter of September 7, 1959) who corresponded with W. M. Hooton, friend of the collector and his companion at the time of the collection. Johnson quotes from Hooton's comments in a letter dated May 26, 1938: "I was looking to the right and he (Charles M.) left, when he saw a larva on a small bush of Buckbrush, nearly mature, very similar to mendocino as regards green background, and tubercles, but these were wine or purplish color with white bars (8) between lowest two of three rows of spots. A second larva turned up later nearby. Five spines in spots as mendo- Bet is is *atlbefasciata*."

Johnson adds: "In a later letter dated June 12, 1938, he (Hooton) says that Charles M. took three larvae. In November-November 15, 1939, he writes that Charles M. took still another larva." Presumably the larvae other than the one which produced the plesio-allotype were lost.

Early Records

Macheboeuf's larvae were not actually the first discovered. The earliest collection of immatures was in 1934 by Johnson himself:

- (4) 1 larva: Stony Camp, Deep Creek Road (Rock Camp, north of Lake Arrowhead), San Bernardino Mountains, San Bernardino County; on buckbrush or similar *Ceanothus*, 12 May 1934 (J. W. Johnson) [specimen lost].

Concerning this collection, Johnson relates (personal communication to Hogue — letter of September 7, 1959), "This spun cocoon exactly like that of *albofasciata*, and produced a small male adult. It hatched while I was away from home and only the battered remains were found months later in the rearing box,...."

W. Bauer and J. S. Buckett add the following records from their collection:

- (5) 1 ♂, 1 ♀ : Clear Lake, Lake County. 24 October 1950 (C. Macheboeuf)
- (6) 1 ♀ : Konocti Bay, Lake County. 24 October 1957 (C. Macheboeuf)

- (7) 2 pupae: Clear Lake, Lake County; ex. *Ceanothus cuneatus*. No date.
(8) 5 eggs: Konocti Bay, Lake County; no host given. 24 October 1957

The only other record prior to 1951 is as follows:

- (9) 1 ♀: Jackson Lake, Big Pines Recreation Park, Los Angeles County; collected at light. 27 October 1950 (John Adams) [Los Angeles County Museum].

Recent Records

The following are the most recent collections and those which have contributed the necessary material for the elucidation of the life history:

- (10) 1 larva (penultimate instar): Kelseyville, 10 mi. W. on road to Hopland, Lake County; beaten from shrub, either *Ceanothus* or *Arctostaphylos*. 20 May 1959 (R. X. Schick) [Los Angeles County Museum].

The specimen was given to one of us (Hogue) by Schick for rearing a few days after it was collected. It molted successfully but died shortly afterwards.

- (11) 1 ♀: 0.2 mi. N. Rock Camp, North of Lake Arrowhead, San Bernardino County; at UV light, temperature 60-70° F., very dry, clear moonless night. 24 October 1959; 7:00 p.m., 1 hour after sunset (F. P. Sala & C. L. Hogue) [Sala].

This female was confined and laid 8 eggs. These and other biological data obtained from rearing this material and that listed in the records to follow are incorporated into the discussions of biology for each stage in a later section.

- (12) 1 larva (early instar): Newcomb's Ranch, San Gabriel Mountains, Los Angeles County; beaten from *Ceanothus* sp. (F. P. Sala) [specimen lost].

- (13) 1 larva (second instar): same locale as above: beaten from *Ceanothus* sp. 5 June 1960. (F. P. Sala) [Sala].

This specimen was successfully reared through to an adult female (emerged 21 October 1960).

- (14) 1 ♀: Same locale as above; at UV light. 21 October 1962; approximately 7:00 p.m. (F. P. Sala) [Sala].

- (15) 1 ♀: Charleton Flat, San Gabriel Mountains, Los Angeles County; resting on flat stone near registration building where some lights were on, specimen lethargic, apparently had been at rest for some time. 22 October 1962; 8:00 p.m. (J. Lane) [Sala].

- (16) 7 ♀ ♀: Willow Creek, near Lake Arrowhead, San Bernardino Mountains, San Bernardino County. 25 October - 5 November 1963. (E. Walter et al.) [Walter].

A large number of eggs were obtained from the 9 preceeding females and reared by Sala (#15) and Walter (#16).

- (17) 1 ♀: near Placerville, El Dorado County, elev. 2000 feet; at UV light. 25 October 1963; 8:00 p.m., 1 hour after sunset (R. Leuschner) [Leuschner].

The specimen was confined but failed to lay any eggs.

- (18) 1 larva (mature): vicinity Wrightwood, San Gabriel Mountains, San Bernardino County; ex. *Ceanothus cordulatus*, June 1963. ♂ emerged October 1963 (W. D. Dyer) [specimens and photographs in Los Angeles County Museum].

By far the largest number of adult specimens have been collected and observed by N. McFarland and C. Henne as follows (some are sight records only):

- (19) 25 ♂♂, 15 ♀♀: White Cliff Ranch, 2.5 mi. SSW. Valyermo, Los Angeles County; elev. 4800 feet. 22 October - 9 November 1963. [McFarland and Henne].
- (20) There are also several records by McFarland and Henne of larvae beaten from *Cercocarpus betuloides* and two particularly interesting observations of males copulating (in the late afternoon) with freshly emerged females sitting on the latter's cocoons which were spun on the same plant.

GEOGRAPHICAL DISTRIBUTION AND HABITAT

All the records of *S. albofasciata* are from mountainous regions, generally through the median elevations (approximately 4500 - 7000 feet) in the Transverse Ranges of southern California, and at lower elevations (down to 1300 feet at Clear Lake) in the northern Coast Ranges and Sierra Nevadas. When known fully, the distributional pattern will probably be found to correspond to that of the host plants. These are species which generally have small, thick leaves and belong to the chaparral or related xerophytic plant communities. Hot, dry summers and freezing (often snow covered) winter periods characterize the climates of these communities at the higher elevations where the moth is found.

The eggs of the moth apparently require freezing to break the winter diapause, an additional factor which no doubt limits the distribution to areas where this requirement is satisfied. In this regard it may be noted that in the southern Transverse Ranges, the moth is known only from the northern, protected and colder, slopes.

DESCRIPTIONS AND BIONOMICS

EGGS (Fig. 1)

Description. Size 1.9 x 1.5 mm.; large for the size of the adult. General proportions, markings and color as figured.

Bionomics. The number of eggs laid per female is not large. The average obtained from a sample of 13 females was only 17.2 with maxima and minima of 36 and 3, respectively.

Confined females lay primarily in the early evening hours between dusk and 9:00 p.m. Oviposition is nearly completed the first evening; a few eggs may be laid a second or third evening.

The eggs are firmly glued to the substratum singly or side by side in short strings of 2 - 10. The natural substratum is not known but probably is the twig bark of the host plants.

Eggs are laid during the fall flight of the adults and remain dormant until the following spring. A pronounced winter ovarian diapause is evident and freezing temperatures are apparently required for a time in order for this stage to develop normally.

MATURE LARVA (Figs. 5-6)

Description. (Only the most characteristic features of the mature larva will be described here; detailed anatomical analysis of all the instars is reserved for future work). Size small for genus, generally only two-thirds the length of *walterorum* or *mendocino*, i.e. 30-45 mm.

Structure, markings and color as figured, the prominent elements as follows: general ground color green; scoli bright pinkish or lavender; bright creamy yellow vertical bars connecting dorso-lateral and lateral scoli on abdominal segments, touching caudal edge of spiracles; conspicuous lanceolate, flat, papery, silvery spines projecting from scoli and integument usually as follows: a single large one from each dorso-lateral scoli on abdominal segments 2-7 and one or two smaller ones from near the bases of the dorsal scoli of segments 1-8; the other scoli spines normal, small, black and bristle-like, some in the form of very long slender hairs.

There is considerable variation in the individual shape, size and distribution of the flat lanceolate spines. Some larvae are completely without them, their places being taken by unmodified, elongate setae. They are always absent from the younger instars.

Bionomics. The larvae hatch in the usual saturniine manner and pass through four instars. Development proceeds uninterrupted by dormant periods of diapause.

The larvae feed externally on the leaves of the host plant. The species of the latter are not known with surety. Larvae have been taken from *Cercocarpus betuloides* Nuttall—Mountain Mahogany (#20) and two species of *Ceanothus* in nature: *C. cordulatus* Kellogg—Snow Bush (Dyer, #18) and *C. cuneatus* (Hooker)—Buck Brush (Macheboeuf and Johnson, #3). *C. Greggii* Gray may be a host in the White Cliff Ranch area where much adult activity was recorded in 1963 and 1964. In the laboratory the larvae feed readily on other species of *Ceanothus* (e.g. *leucodermis* Greene and *spinosus* Nuttall), and *Fremontia californica* Torrey, also a chaparral species.

These facts imply that a wide range of chaparral plants may serve as hosts. This tendency is evident in other *Saturnia* species, including the close relatives of *albofasciata* (Sala and Hogue,

1958:24). These moths seem to exemplify cases of larval adaptation to a plant community rather than to a single plant species or taxonomic group as is most often the case.

The larvae are not especially active, and crawl slowly. They are extremely delicate in captivity. Rearing conditions must be closely controlled: food must be very fresh; the larvae must have 2 or more hours of sunlight and semi-shade, and moving air, every day. McFarland found it advantageous to cover the rearing cages with plastic bags indoors to prevent dehydration when the food plant begins to wilt. In spite of such careful handling, McFarland succeeded one season in obtaining only 14 pupae from 108 eggs. It is evident that the larvae have certain requirements that are not yet understood.

PUPA AND COCOON (Fig. 2)

Descriptions. Pupa small for genus, length approximately 13 mm. Cremaster with single spine.

Cocoon very different from *walterorum* or *mendocino*; size small, length 20-25 mm.; color variable: pale sulfur yellow to yellowish-orange, usually "salmon-orange," occasionally dull brown; wall tough, texture smooth or slightly wrinkled with closely spun single wall (without the loose, outer fenestrate weir of *walterorum*, *mendocino*, and *Agapema*); emergence exit pre-existent, of the "draw-string" type.

Bionomics. The cocoons are formed in the early summer (late June-early July). The species remains in this stage until late October, the time of emergence and adult activity. Thus there is regularly a second period of diapause-like dormancy in the life cycle of this species.

ADULTS (Figs. 3-4)

Descriptions. The adults are adequately described and figured by Johnson in his original papers (1938; 1940) and his black and white photographs in the latter paper readily permit recognition of both sexes of this unique *Saturnia*. Our figures 3 and 4 are provided so that the colors may be appreciated.

The wing patterns bear an interesting relationship to the other American members of the genus. With regards to the upper surfaces only, the *male* pattern and color closely mimic that of *S. (Calosaturnia) walterorum* and *mendocino*. The major exception is the white bar midway along the inner area projecting towards the ocellus. This bar is also present in the female, but, unlike the male, reaches the ocellus and has a mate in the hind wing. It apparently represents the proximally displaced, caudal sector of the TP line. The ground color of the hind wings

of the male also are much redder than the pure orange of the other species. The overall pattern and colors of the *female* pattern are like those of the subgenus *Agapema*, especially *A. galbina*.

From these characters, *albofasciata* can be thought to occupy an intermediate morphological position between the other two species of *Calosaturnia* and species in the genus *Agapema*. This intermediacy is demonstrated as well by other structural and behavioral characteristics (See Table 1).

These facts make possible some interesting speculation regarding the phylogenetic history of the American *Saturnia* from which may be derived a better interpretation of the taxonomic status of *albofasciata* than presently stands. These will be considered in the following section.

The male genitalia of *albofasciata* are like those of other *Calosaturnia* in lacking a sclerotized aedeagus.

Bionomics. The adults are active in the fall of the year, primarily in late October and early November. The females are crepuscular and nocturnal (early evening); the males fly during mid- and late afternoon. As indicated by confined specimens, and those taken at light, the females fly into the early evening during which time they oviposit. They settle down by late evening and are inactive through the rest of the night and following day. The males actively seek out "calling" females in the late afternoon and copulation takes place where the latter are found. Copulation probably stimulates the female to flight and oviposition.

The flight characteristics of the male are similar to those described for *S. (Calosaturnia) walterorum* (Sala and Hogue, 1958:18). The moths fly very rapidly, 3-10 feet above the ground, dodging and bobbing erratically. This, plus the usually rough terrain of their habitat, make them difficult to net. They are particularly quick to react to the sound of a snapping twig, or a bush brushed by the collector.

Collecting is productive for females with lights set out just at dusk. They are attracted to both Coleman lantern and black light.

CHRONOLOGY OF THE LIFE CYCLE

One brood per year

Mid-fall (late October): adults emerging and active. Eggs laid.

Late fall-winter (November-April): eggs dormant. (ovarian diapause).

S. (Calosaturnia)		S. (Calosaturnia)		S. (Agapema)	
mendocino and walterorum		albofasciata		galbina and homogena	
♂	♀	♂	♀	♂	♀
1. diurnal	1. diurnal	1. diurnal	1. nocturnal	1. nocturnal	1. nocturnal
2. eyes small	2. eyes small	2. eyes small	2. eyes large	2. eyes large	2. eyes large
3. antennae bipectinate	3. antennae bipectinate	3. distal rami partially developed	3. antennae quadri- pectinate	3. antennae quadri- pectinate	3. antennae quadri- pectinate
4. brightly colored	4. brightly colored	4. brightly colored	4. dull colored	4. dull colored	4. dull colored

Table 1: Comparative anatomy and behavior of S. (Calosaturnia) and S. (Agapema)

Early spring (April-May): eggs hatch.

Late spring-early summer (April-June): period of larval development.

Early summer (late June-early July): spinning and pupation.

Summer-mid-fall (July-late October): pupal period. (pupal diapause).

There are some questions raised by this unique life cycle pattern: Firstly, how does it relate phylogenetically to the patterns of the species' close relatives, especially the dual dormancy (diapause?) phase? In this regard, it is interesting to note that the pupal state of *albofasciata* has the pre-emergence development phase much the same as *walterorum*, and no doubt *mendocino*.

Secondly, what is the relationship of the ovarian period of dormancy to the pupal dormancy in this moth—and for that matter in other Lepidoptera and insects? Demonstrated again is the need for a better definition of the terms diapause and dormancy.

PHYLOGENETIC CONSIDERATIONS AND TAXONOMY

The genus *Saturnia* (sensu Michener 1952:477) is represented in America by only five species grouped into two subgenera: (*Calosaturnia*) *albofasciata* (Johnson), *mendocino* (Behrens), *walterorum* Hogue and Johnson (*meridionalis* of Johnson); (*Agapema*) *galbina* (Clemens) (including three subspecies) and *homogena* Dyar. The genus is well developed, by contrast, in the Old World. It seems certain that the ancestor of our species migrated here from Asia relatively late in saturniine evolution (Michener 1952:371). The subsequent pattern of divergence taken by descendents of the ancestor which produced our present species is, of course, unknown but can be inferred from their comparative anatomy and behavior. Assisted by the foregoing new information on *albofasciata*, we are able to suggest the following as the most likely hypothesis:

The Old World subgenus *Eudia* is closest to *Calosaturnia* and *Agapema* structurally. A single ancestral form probably resembling types like *Saturnia* (*Eudia*) *pavonia* or *spini* migrated into the mountainous Pacific region of North America by way of a past Bering land connection. The amazingly close parallelisms in wing color and bionomics which exist between *pavonia* and *albofasciata* strongly suggest very close relationship, possibly even a common ancestor quite like both of them, but probably tending more toward *pavonia* which exhibits the more primitive

anatomy (e.g. "noctuiform" wing pattern, sclerotized aedeagus, larger size, etc.).

This ancestral form probably was adapted to cool, dry mountain climates and the larvae fed on shrubs as do *pavonia*, *walterorum* and *mendocino* presently. We would speculate also that the males were diurnal and the females nocturnal. Derived from this ancestor are our current two distinct lines *Calosaturnia mendocino* and *walterorum*, on the one hand, in which both sexes are diurnal and brightly colored and *Agapema*, on the other hand, in which both sexes are nocturnal and dull colored.

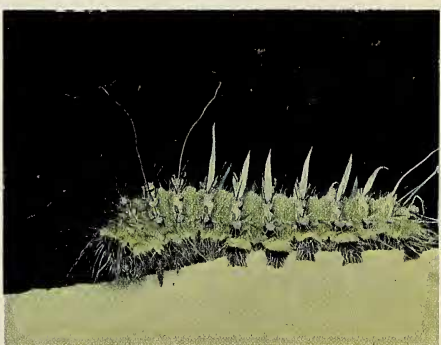
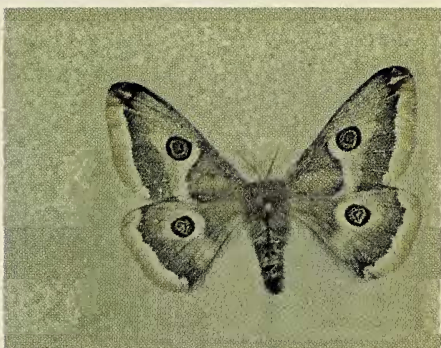
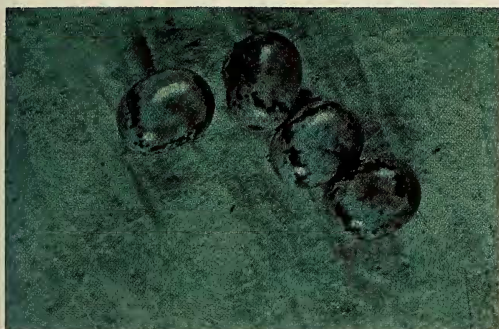
It is, to say the least, highly precarious to attempt an explanation of the origin of this dichotomy without some investigation of the genetics of the species concerned. Yet we would like to cautiously suggest that the two lines arose directly out of the sexual dimorphism of the adults. Besides *pavonia* and *albofasciata* there are other examples among bombycoid moths in which the males (usually with rust or reddish wings) are diurnal and more brightly colored than the females which are nocturnal and dull colored (usually light grey or brown): *Endromis versicolora* (Endromididae; Palaearctic), *Aglia tau* (Saturniidae; Palaearctic), *Polythysana andromeda* (Saturniidae; Chile).

The males and females of such species are actually considerably divergent morphologically and behaviorally. It is conceivable that individuals of both sexes would appear with characteristics more similar to the opposite sex. Some of these characteristics might affect mating frequency so that like individuals would tend to cross more readily than unlike, e.g., mutant night-flying males might encounter more females also in flight than normal males would resting, motionless females, or brightly colored females might appear which would be more easily encountered by males during the day than the dull colored normals.

Other factors would tend to complicate these simple examples, such as pheromone effectiveness, predator attention, visual acuity, etc., but we think it not too far wrong to postulate divergent populations, (species and even genera) developing from such anomalies, with their total members more similar than the normal sexes of *albofasciata* are different.

ACKNOWLEDGMENTS

We wish to thank John Johnson, Corona del Mar, for contributing the information necessary to reconstruct the early records and knowledge of the species. The following persons



Figures 1-6: *Saturnia albofasciata* Johnson.

1: Eggs. 2: Cocoon. 3: Adult male (live specimen). 4: Adult female. 5: Mature larva. 6: Newly molted final instar larva, showing dorso-lateral lanceolate spines particularly well.

generously made available records from their own collections: William Bauer, Petaluma; Steve Buckett, Petaluma; W. David Dyer, Los Angeles; John Lane, Los Angeles; Ronald Leuschner, Gardena; Erich Walter, Anaheim. We also acknowledge the assistance of Leonila Vázquez G., Mexico City, for checking the type material of *Saturnia albofasciata* for us during her visit to the California Academy of Sciences in 1962.

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